Decaying Logs Enrich Soil Fungal Communities in the Forest Ecosystem

Qin Wang

Taizhou University

Josep Peñuelas

Global Ecology Unit CREAF-CSIC-UAB, CSIC

Bo Tan

Sichuan Agricultural University

Zhuang Wang

Sichuan Agricultural University

Han Li

Sichuan Agricultural University

Rui Cao

Sichuan Agricultural University

Chenhui Chang

Sichuan Agricultural University

Yurui Jiang

Sichuan Agricultural University

Wanqin Yang (✉ scyangwq@163.com)

Taizhou University <https://orcid.org/0000-0003-1051-8607>

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Abstract

Aims:

Soil fungi are crucial drivers of log decomposition in forest ecosystems. The objective of this study was thus to assess the conservation roles of decaying logs on soil fungi.

Methods:

Five classes of decaying Minjiang fir (*Abies faxoniana*) logs were incubated on the forest floor in a subalpine coniferous forest on the eastern Qinghai-Tibet Plateau, China, and the fungal communities compositions of the soil under decaying logs were assessed using high-throughput sequencing.

Results:

A total of 4321 operational taxonomic units (OTUs) were detected by Illumina MiSeq sequencing analysis. Basidiomycota and Ascomycota were dominant phyla regardless of log decay classes. With the log decomposition, the proportion of arbuscular mycorrhiza, wood saprotroph and saprotroph increased, but that of ectomycorrhiza decreased. Moreover, the diversity of soil fungal communities also increased along the decomposing process of logs. The decaying logs significantly altered soil fungal community composition by affecting biochemical properties (e.g. pH and concentrations of microbial biomass nitrogen and total phosphorus) and environmental factors (e.g. soil water content).

Conclusion:

Different decay classes of logs favor special fungal species, implying that the logs conservation with different decay classes in the forest ecosystem is of great significance for improving the diversity of soil fungi.

1. Introduction

Decaying logs are an important habitat for many organisms and play crucial roles in the global carbon cycle, soil formation, and water and soil conservation (Lassauce et al. 2011). The decomposition of logs is believed to be mainly carried out by fungi, whose hyphae can penetrate into the woody debris and secrete extracellular enzymes to decompose refractory organics such as lignocellulose (Baldrian and Banin 2017), finally release soluble substrates for microbial uptake (Moorhead et al. 2012). The logs are in direct contact with the soil surface and therefore might alter the structure of the fungal community of the underlying soil during the decomposition process. Zalamea et al. (2016) and Semchenko et al. (2018) have reported that the decomposition of logs directly affects the physical, chemical and biological properties of the soil under the logs. Minnich et al. (2021) have also found that deadwood can affect soil microbial community structure. Previous studies have reported the role of deadwood in the conservation of macrofungi, plants and invertebrates (Bani et al. 2018), but the responses of the composition and functional groups of soil fungal community to the decomposition of logs have rarely been studied.

Soil fungi are key participants in the biogeochemical cycles of forest ecosystems, playing essential roles in the formation and development of soil, storage of soil carbon (C), nutrient cycling and energy flow (Tedersoo et al. 2014). The role of the soil fungal community is closely related to its structure and diversity, and the structure and diversity of the soil fungal community are affected by biological and abiotic factors such as hydrothermal environment, substrate quality and microbial eaters (Franklin and Mills 2009; Asemaninejad et al. 2018). Lindahl et al. (2007) have observed that the presence of wood-rotting fungi in the soil, such as saprotrophic fungi, which are the main factor in decomposing organic matter and are critical in regulating nutrient cycling. Some fungal species are even found only in the soil under the decaying wood (Makipaa et al. 2017). In addition, some mycorrhizal fungi have the ability to colonize the wood substrate in contact with the soil surface, mineralize organic matter, and even tend to produce fruit bodies more often in wood than in soil (Lindahl and Tunlid 2015). Makipaa et al. (2017) have demonstrated that the structure of soil microbial communities under decaying logs at the initial stage of decomposition is relatively simple, but highly decayed wood released more ions into the surface layers of the soil than did less-decomposed wood (Jarosław et al. 2017). The stage of decomposition of deadwood affects the C:N:P stoichiometry of the soil (Wojciech et al. 2019), which may further cause the differences in soil fungal community structure. Thereby, the composition and diversity of soil fungal community might be closely correlated with log decay process, and affect the formation of soil organic matter.

Affected by the limitation of low temperature and frequent geological disasters, the soil in the subalpine forest on the eastern Qinghai-Tibet Plateau develops slowly and is often blocked (Yang and Wu 2021). Therefore, the organic layer of the soil and the decaying logs on the ground play an irreplaceable role in biodiversity conservation, material circulation, and water and soil conservation. The goal of this study was to analyze the effects of decaying logs on the composition of soil fungal communities and the response of the fungal community and functional groups to the heterogeneity of decay classes. We hypothesized that (1) decaying logs favor different groups of soil fungi thus enriching soil fungal communities; and (2) decaying logs would affect the fungal communities by altering soil biochemical properties and/or environmental factors. We tested these hypotheses by incubating decaying logs in a subalpine coniferous forest on the eastern Qinghai-Tibet Plateau, China. Minjiang fir (*Abies faxoniana*) is the dominant tree species in this region. Minjiang fir logs at various stages of decay were incubated for six years on the forest floor, and the compositions of the soil fungal communities in the soil under the logs were determined using high-throughput sequencing. The objective of this study was thus to assess the conservation roles of decaying logs on soil fungi.

2. Materials And Methods

2.1 Site description

The study was conducted at the Long-Term Research Station of Alpine Forest Ecosystems (31°14'-31°19'N, 102°53'-102°57'E; 2458-4619 m a.s.l.) in Li County, Sichuan Province, southwestern China. The region is a transitional area between the Tibetan Plateau and the Sichuan Basin. The annual

mean temperature and precipitation are approximately 2-4°C and 850 mm, respectively (Chang et al. 2019). The seasonal soil freeze-thaw period begins in early November and ends in April the following year. The soil is classified as Cambisols and Primosols (Xiao et al. 2014). The accumulation of large amounts of woody debris (53 t·ha⁻¹) in this region (Xiao et al. 2016) plays crucial roles in maintaining soil fertility, controlling soil erosion and promoting biodiversity. The trees consist mainly of Minjiang fir (*Abies faxoniana*), cypress (*Sabina saltuaria*), larch (*Larix mastersiana*) and red birch (*Betula albo-sinensis*), with Minjiang fir accounting for 80% of the total basal area at the site (Xiao et al. 2014). The main understory shrubs include willow (*Salix paraplesia*) and azalea (*Rhododendron lapponicum*).

2.2 Experimental design

We established a permanent 100 × 100 m plot of primary Minjiang fir forest in the nature reserve in August 2013 based on previous studies (Chang et al. 2019; Chang et al. 2020) and three 25 × 25 m subplots with similar slope aspects, slope degrees, canopy closures and tree heights. Logs 35 ± 5 cm in diameter in five classes of decay (I-V, at increasing levels of decay) described in detail by Chang et al. (2019) and Wang et al. (2021) were collected. The logs of decay class I were from newly felled trees, representing the start of decomposition, and the logs of classes II-V were collected from the primary coniferous forest. All logs were sawed on-site into lengths of 120 cm and carefully placed into the closed canopy in each subplot. Six sections of the logs in the same decay class were incubated on the forest floor in each subplot. See Chang et al. (2020) and Wang et al. (2021) for more details. This experiment studied the three sections where epiphytic vegetation was not removed.

2.3 Sampling

Soil samples were collected in August 2019 from the 0-10 cm layer in each subplot using an auger (5 cm diameter) after the decaying logs were carefully removed. Control samples (CK) were also collected >3 m from the decaying logs. The samples were transported to the laboratory on ice packs in a cooler. A total of 54 soil samples were collected [(1 CK + 5 decay classes) × 3 replicates × 3 subplots]. Visible living plant material was removed from the samples, and about 20 g of soil was used to determine the water content (WC). The samples were passed through a 2-mm sieve, and subsamples were stored at -70 and 4°C for molecular and biochemical analysis, respectively. The remaining subsamples were air-dried and passed through 0.149-mm sieves, placed in sealable bags and stored at room temperature for elemental analysis. Five of the nine replicate samples were randomly selected, for a total of 30 samples.

2.4 Soil physiochemical and biological analyses

Water content was determined by weighing the samples before and after drying. Soil pH was measured using a pH meter at a soil: water ratio of 1:2.5 (m/v). The concentrations of organic C (OC), total nitrogen (TN) and total phosphorus (TP) in soil were measured using potassium dichromate oxidation-ferrous sulfate titrimetry, Kjeldahl determination and molybdenum-antimony colorimetry, respectively (Lu 1999). Soil microbial biomass C (MBC) and microbial biomass nitrogen (MBN) were measured using chloroform fumigation and K₂SO₄ extraction (Brookes et al. 1985; Vance et al. 1987). Soil microbial biomass

phosphorus (MBP) was measured using chloroform fumigation and NaHCO_3 extraction (Brookes et al. 1982).

2.5 DNA extraction, PCR amplification and high-throughput sequencing

Microbial DNA was extracted from the samples using the FastDNA Spin Kit for Soil (MP Biomedicals, Solon, USA) following the manufacturer's instructions. DNA was checked for quality using agarose gel electrophoresis and ultraviolet absorbance (ND1000, Nanodrop, Thermo Fisher Scientific, Waltham Mass, USA). The DNA was diluted to 1 ng/ μl using sterile water and stored at -20°C until analysis.

A region of the fungal ITS2 gene was amplified, purified, quantified, pooled and sequenced on an Illumina NovaSeq platform at Novogene Genomics Institute (Beijing, China). The fungal ITS2 gene was amplified using the primer pair ITS3-2024F (GCATCGATGAAGAACGCAGC)/ITS4-2409R (TCCTCCGCTTATTGATATGC). PCR products were detected by electrophoresis in a 2% (w/v) agarose gel, and bands were excised, mixed in equal density ratios and purified using a GeneJET Gel Extraction Kit (Thermo Fisher Scientific, Waltham Mass, USA). The purified PCR products were sequenced on the Illumina NovaSeq platform by Pair-End (When constructing the DNA library to be tested, binding sites of sequencing primer were added on the adapters at both ends). The raw data were then controlled for quality using UPARSE. USEARCH was used to identify and remove chimeras, and the remaining sequences were clustered to generate operational taxonomic units (OTUs) at the 97% similarity level (Edgar 2010; Magoč and Salzberg 2011). Quantitative Insights Into Microbial Ecology (QIIME) was used to process and analyze the high-quality sequences (Kuczynski et al. 2011). Representative sequences were deposited in the UNITE database for fungi.

In addition to taxonomic composition, the fungal functional groups were further anticipated based on FUNGuild (Nguyen et al. 2016). The fungi could be assigned to a guild with the confidence level of "probable" or "highly probable". We classified the fungal taxa into six functional groups (i.e., animal pathogen, arbuscular mycorrhiza, ectomycorrhiza, plant pathogen, wood saprotroph and saprotroph) with some overlaps. This functional prediction method is broadly used to realize soil fungal communities (Pfennigwerth et al. 2018; Semchenko et al. 2018).

2.6 Statistical analyses

We used one-way ANOVAs to test the effect of the extent of decay on the concentrations of MBC, MBN, MBP, OC, TN and TP. The diversity indices (Shannon and Simpson) and richness estimators (Chao1 and abundance-based coverage estimator (ACE)), metrics of alpha diversity of the soil fungal communities, were calculated. The effects of the decay classes on fungal community structure were further tested using nonmetric multidimensional scaling (NMDS) with OTUs. Heatmap was used to show compositions of fungal functional groups inferred by FUNGuild from different decay classes of logs. Spearman correlation analysis was used to identify relationships between soil physicochemical properties and the relative abundances of fungal taxa. The metrics of alpha diversity and the NMDS, heatmap and

Spearman analyses were performed using the VEGAN package (Oksanen et al. 2013) in R (R Development Core Team 2015). Other statistical analyses were performed using SPSS 20.0 (IBM Corporation, Armonk, USA). The statistical tests were considered significant at $P < 0.05$.

3. Results

3.1 Soil microbial biomass and C, N, and P concentrations

The soil concentrations of MBN, MBP, OC, TN and TP were significantly higher in the higher decay classes ($P < 0.01$), but the MBC concentration did not differ significantly among the classes ($P = 0.052$) (Fig. 1). The concentrations of microbial biomass, OC and TN were higher in the soil under the decaying logs than in CK. The much higher concentrations of MBN, MBP, OC and TN relative to CK began in classes III, II, II and I, respectively. The TP concentration was lower in the soil under the decaying logs in classes I-III than in CK but did not differ significantly between classes IV and V and CK.

3.2 Characteristics of the sequence data and species alpha diversity

Pyrosequencing of 30 soil samples under decaying logs produced total 3 344 637 raw fungal sequences, and 1 926 264 high-quality fungal sequences were retained after the raw sequences were controlled for quality. The sequence data were classified into 4321 fungal OTUs at a cutoff in sequence similarity of 97%. The Shannon-Wiener and Simpson diversity indices for the fungal communities differed significantly among the decay classes ($P < 0.05$) and were the highest for DC3 and DC4. The number of OTUs and the Chao1 and ACE richness indices for the fungal community, however, did not differ significantly among the classes or between CK and the soil under the decaying logs ($P > 0.05$) (Table 1). However, no difference in OTUs and richness (Chao1 and ACE indices) of soil fungal community was observed between log decay classes, neither between the soil samples of blank control group versus soil under decaying logs ($P > 0.05$). The number of unique fungal OTUs was higher under the decaying logs than CK (except for DC4) (Fig. S1).

Table 1
Number of operational taxonomic units (OTUs) and indices of alpha diversity for the fungal communities in the soil under decaying logs for the decay classes (mean $\pm$ *SD*, *n* = 5). CK, control; DC1-DC5, decay classes I-V. Different letters within a column indicate significant differences (*P* < 0.05) among the classes.

Class	No. OTUs	Shannon	Simpson	Chao1	ACE
CK	607 $\pm$ 199a	3.84 $\pm$ 0.72b	0.734 $\pm$ 0.055c	1265 $\pm$ 395a	1051 $\pm$ 319a
DC1	684 $\pm$ 48a	4.63 $\pm$ 0.40b	0.832 $\pm$ 0.050b	1394 $\pm$ 129a	1132 $\pm$ 97a
DC2	663 $\pm$ 166a	3.76 $\pm$ 0.48b	0.722 $\pm$ 0.053c	1476 $\pm$ 467a	1200 $\pm$ 290a
DC3	845 $\pm$ 160a	6.14 $\pm$ 0.45a	0.9551 $\pm$ 0.016a	1467 $\pm$ 381a	1245 $\pm$ 275a
DC4	790 $\pm$ 178a	6.07 $\pm$ 0.92a	0.954 $\pm$ 0.029a	1539 $\pm$ 767a	1198 $\pm$ 342a
DC5	890 $\pm$ 115a	5.94 $\pm$ 1.09a	0.929 $\pm$ 0.059a	1637 $\pm$ 164a	1355 $\pm$ 119a

3.3 Taxonomic composition of fungi

Basidiomycota (22.0-49.3%), Ascomycota (15.7-41.5%) and Mortierellomycota (2.4-11.9%) were the most dominant fungal phyla, representing >65% of the total reads (Fig. 2a). The relative abundance of Mortierellomycota was significantly higher in the soil under the decaying logs than in CK and was the lowest in DC2 and the highest in DC4 (*P* < 0.05). The relative abundance of Basidiomycota decreased as the decay class increased, and Ascomycota had the opposite trend, but the relative abundances of Basidiomycota and Ascomycota did not differ significantly among the classes (Figs. 2a and S2a). The relative abundances of other phyla, including Rozellomycota, Glomeromycota, Chytridiomycota and Mucoromycota, were <1%. The relative abundances of all these phyla except Mucoromycota were significantly affected by the decaying logs.

A total of 24 fungal genera (relative abundance >1%) were identified across all samples (Fig. 2b). Piloderma, Inocybe and Mortierella were the three most abundant genera. The relative abundance of Piloderma was higher (except for DC5), the relative abundance of Inocybe was lower (except for DC3) and the relative abundance of Mortierella was higher in the soil under the decaying logs than in CK (Figs. 2b and S2b). The relative abundances of most of the other genera, such as Ilyonectria, Fusarium, Sebacina, Russula, Phlebia, Humicola and Pleotrichocladium, were significantly higher for the decay classes than CK (Fig. S2b).

NMDS of Bray-Curtis distances was used to compare the similarity of the soil fungi between CK and the decay classes (Fig. 3a). The taxonomic composition of the soil fungal communities differed significantly among the classes (stress <0.2).

3.4 Compositions of fungal functional group inferred by FUNGuild

The relative abundance of most putative fungal functional groups was significantly affected across the treatments (Fig. 4). The proportion of arbuscular mycorrhiza, wood saprotroph and saprotroph increased with the increase of the decay classes of logs, while the proportion of ectomycorrhiza decreased. Additionally, the relative abundance of wood saprotroph did not differ between CK and decay classes I-III but increased drastically at decay class IV. The relative abundance of animal pathogen reached its maximum value at the decay classes IV, while the relative abundance of plant pathogen reached its maximum value at the decay classes III. Heatmap of soil fungal functional groups showed that the soil under the decay class I of logs and the soil at CK were gathered into the same branch, and the soil under decay class IV and V of logs were gathered into the same branch (Fig. 3b).

3.5 Correlations between fungal taxonomic composition and soil biochemical properties

Spearman correlation heatmaps were analyzed to identify the relationships of the fungal communities with biochemical properties and environmental factors (Fig. 5). Soil pH and the concentrations of MBC, MBN and TP and were important factors influencing the relative abundances of Basidiomycota and Ascomycota (the two phyla with the highest relative abundances) and were correlated positively with the relative abundance of Basidiomycota but negatively with the relative abundances of Ascomycota, Glomeromycota and Chytridiomycota (except for pH) (Fig. 5a). Water content and the concentrations of MBC, MBN and TP were negatively correlated with the relative abundances of the genera *Ilyonectria*, *Fusarium*, *Humicola*, *Pleotrichocladium*, *Chaetomium*, *Tetracladium*, *Dactylonectria*, and *Didymosphaeria*, but the concentrations of MBC, MBN, MBP and OC were positively correlated with the relative abundances of *Cortinarius* and *Meliniomyces*. pH was positively correlated with the relative abundances of *Ilyonectria*, *Fusarium*, *Humicola*, *Pleotrichocladium*, *Chaetomium*, *Tetracladium* and *Dactylonectria* (Fig. 5b).

4. Discussion

Decaying logs contribute greatly to the overall compositions of soil fungal communities. Logs increased the diversity of the fungal communities, thereby altering their compositions, consistent with our hypotheses. The diversity of the soil fungal community increased as the decay class increased. The decaying logs, however, did not affect the richness of the soil fungal community and the relative abundance of dominant species. The proportion of functional groups varied with decay classes of logs, indicating that decaying logs favor different functional groups of soil fungi, rather than dominant species thus enriching soil fungal communities. The composition of fungal communities of the soil under decaying logs was closely related to biochemical properties (e.g. pH, concentrations of microbial biomass nitrogen and total phosphorus) and environmental factors (e.g. soil water content). Our results indicated the conservation of logs with different decay classes in the forest ecosystem is of great significance for improving the diversity of soil fungi.

4.1 Variation of biochemical properties in soil under decaying logs

The soil concentrations of MBN, MBP, OC and TN were higher under the decaying logs than in CK. Previous studies have reported the same trend. Kappes et al. (2007) have found that the presence of coarse woody debris improved the chemical and biotic parameters of soil in acidified broadleaved forests. Adamczyk et al. (2016) have reported that the removal of coarse woody residue negatively affected the soil microbial biomass and net N mineralization, since the decomposition and use of decaying logs by soil microorganisms break organic matter down into inorganic substances and participates in soil processes through the debris food chain. The concentrations of MBN, MBP, OC, TN and TP in the soil under decaying logs also increased significantly with the decay class, indicating that the heterogeneity among the decay classes significantly affected the biochemical properties of the soil (Wojciech et al. 2019). MBC concentration, however, did not differ significantly among the classes, implying that the effect of decaying logs was probably more important for the acquisition by soil microbes of N than C (Adamczyk et al. 2016).

4.2 The diversity of soil fungal communities increased along the log decomposition

The Shannon-Wiener and Simpson indices for the soil fungal communities differed significantly among the decay classes and were the highest in the late stage of decay, suggesting that the fungal communities in the soil under the decaying logs increased in species richness during the decay of the logs. The results for fungi were consistent with those reported by Makipaa et al. (2017), who found that the fungal community in the wood was more similar to that in the soil in the late stage of decay than early stage of decomposition and that some microbial species occurred in the soil only when decaying logs were present on the soil surface. Decaying logs serve as an additional source of nutrients but also provide a more stable moisture content of the soil surface in the late stage of decay (Zalamea et al. 2016), offering beneficial habitat conditions for some mycorrhizal species. The Chao1 and ACE richness indices for the soil fungal community in our study did not differ significantly among the decay classes. The presence of the decaying logs, especially highly decayed logs, thus affected the composition of soil microbial communities.

4.3 Effect of decaying logs on taxonomic composition of soil fungi

Basidiomycota and Ascomycota were the two dominant phyla across CK and all decay classes, consistent with a previous study (Chen et al. 2017). Other studies have reported that exogenous materials such as plant litter and wood were the main sources of C for Basidiomycota, which can degrade lignin and humic acids (Purahong et al. 2016), but the relative abundance of Basidiomycota in our study did not differ significantly between the soil under the decaying logs and CK, indicating that the abundance of dominant fungal species is determined by the regional climate and soil type. The relative abundance of

Basidiomycetes and Ascomycetes was generally lower in the soil under the decaying logs than in CK, perhaps owing to some wood-decaying fungi can colonize the soil, thereby increasing fungal diversity under decaying logs and decreasing the relative abundances of these two groups of fungi. The relative abundances of some Basidiomycota genera, such as *Piloderma*, *Inocybe*, *Sebacina*, *Russula* and *Phlebia*, and that of some Ascomycete genera, such as *Ilyonectria*, *Fusarium*, *Humicola* and *Pleotrichocladium* (Fig. S3), however, differed significantly among the decay classes, indicating that, in addition to mycorrhizal capacity, these soil fungi also have the capacity to decompose wood. Previous studies have demonstrated that some mycorrhizal groups have retained mechanisms of decomposition similar to those of brown- and white-rot fungi and actively participate in the decomposition of organic matter (Lindahl and Tunlid 2015). Mortierellomycota, a typical species found in soil (Lindahl et al. 2007), was as abundant in heavily decayed wood as in soil (Makipaa et al. 2017). Some phyla with lower relative abundances in our study were also significantly differentially represented in the decay classes. Decaying logs are thus an important source of nutrients for some soil fungal communities.

4.4 Response of soil fungal functional group to log decomposition

According to the classification results of FUNGuild, the relative abundance of fungal functional groups varied with the trophic mode in the decomposing process of logs. Pathogenic, saprotrophic, and symbiotic fungi can drive plant-soil feedbacks in complex ways (Semchenko et al. 2018). Pathogenic fungi obtained nutrients by damaging host cells. The results implied that pathogenic fungi colonized on decaying logs at the initial stage of decomposition, and began to damage plant cells in a large amount in the intermediate stage of decomposition. Wojciech et al. (2019) have demonstrated that the logs in the first and second stages of decay, without clear signs of decomposition. Besides, the soil under Minjiang fir decaying logs was dominated by saprotrophic fungi. Wood saprotroph and saprotroph were heterotrophic organisms that obtain a major fraction of their metabolic carbon from dead organic matter (Lindahl and Tundia 2015). Previous studies have shown that soft-rot fungi were common in the early stages but white- and brown-rot fungi became dominant as decay progressed (Rajala et al. 2011). In this study, the relative abundance of wood saprotroph and saprotroph increased drastically at decay class IV, indicating that more saprophytes were needed to decompose refractory organics such as lignocellulose at the highly decayed logs.

Arbuscular mycorrhizal fungi acquired carbon from host plants and obtained substantial amounts of nitrogen from decomposing organic materials (Hodge and Fitter 2010), and deliver mineral nutrients to the host, in particular phosphate (Ezawa and Saito 2018). Coline et al. (2018) have shown that water availability played a key role in affecting soil arbuscular mycorrhizal fungi. Therefore, with the increase of nutrients and moisture content, the relative abundance of Arbuscular mycorrhizal fungi increased with the decomposing process of logs. Our findings are contrary to previous studies that have demonstrated that ectomycorrhizal fungi became the most abundant group in the late stages of succession (Rajala et al. 2011). Lindahl and Tunlid (2015) have proposed that ectomycorrhizal fungi do not regularly use organic matter as a source of metabolic carbon, but rather that their access to host sugars facilitates co-

metabolic degradation of complex, recalcitrant organic complexes, thereby releasing N from organic pools, which may explain why ectomycorrhizal fungi are less affected by the decay classes of logs. In addition to the changes in soil nutrients and environmental conditions, the interaction between fungi with different trophic modes also affected the proportion of fungal functional groups (Lindahl et al. 1999). The results indicated that logs with different decay classes conserved different soil fungi groups.

4.5 Influencing factors of soil fungal community composition

Organic matter is an important component of soil, and its concentration strongly affects the structure and function of soil microbial communities (Grayston et al. 2004; Franklin and Mills 2009). The composition of soil OC affects the abundance and structure of microbial communities (Zhang et al. 2020). N addition can also alter the composition of soil fungal communities, such as symbiotic mycorrhizal fungi (Morrison et al. 2016; Corrales et al. 2017). The concentrations of OC and TN in our study were poorly correlated with the relative abundances of the soil microorganisms, but the concentrations of MBC and MBN significantly affected the relative abundances of fungi, perhaps due to the role of highly heterotrophic metabolic microorganisms such as saprophytes. Changes to the concentrations of MBC and MBN could then better represent the dynamic changes of microorganisms in soil under decaying logs than could the concentrations of OC and TN. The concentration of TP is among the main factors influencing microbial activity at regional spatial scales (Cao et al. 2016). The concentration of TP in our study was significantly correlated with the relative abundances of some of the fungal communities. Similar observations were also reported for soil planted with Chinese kale (Pongsilp and Nimnoi 2020). The significant differences in MBC, OC and TP concentrations among the decay classes may to some extent account for the separation of Glomeromycota.

Soil pH is also a critical factor for the diversification of fungi and strongly influences the structure of soil microbial communities (Geisseler and Scow 2014). pH can directly affect soil microbial communities and indirectly affect the structure of some microbial communities through interactions among soil elements (e.g. precipitation of ions) (Lammel et al. 2018). The dominance of some phyla in our study, such as Basidiomycetes and Ascomycetes, depended strongly on soil pH. Water content was also strongly correlated with the characteristics of the microbial communities (Brockett et al. 2012). These results indicated that the dominant fungi in the soil under decaying logs might respond to the changes in water content by the allocation of limited resources.

Conclusion

This study examined the effects of decaying logs on the composition of soil fungal communities in a subalpine forest. Our results showed that decaying logs affected the compositions of soil fungi and enrich soil fungal communities. The abundances of the dominant species of soil fungi were not significantly affected by the decomposition of the logs, indicating that the soil fungi could maintain stable community structures by self-regulation. Additionally, decaying logs favor different functional

groups of soil fungi, and fungal functional groups of soil under highly decayed logs tended to be similar. Biochemical properties (e.g. pH, the concentrations of MBN and TP) and environmental factors (e.g. water content) in our study accounted to some extent for the heterogeneity of the fungal communities among the decay classes. Therefore, the conservation of logs with different decay classes in the forest ecosystem is of great significance for improving the diversity of soil fungi. Log decomposition is a long-term and complex biological process, so the response of soil microorganisms to the decomposition of logs needs long-term experimental research.

Declarations

Author contributions

W.Q.Y. and B.T. conceived and designed the experiment and contributed resources. Q.W. completed laboratory analysis and led the writing of the manuscript. Q.W., B.T., Z.W., H.L., R.C., C.H.C., and Y.R.J. contributed to field work. W.Q.Y., and J.P. provided writing assistance. All authors have read and agreed to the published version of the manuscript.

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Declaration of competing interest

All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript.

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Figures

Figure 1

Concentrations of microbial biomass carbon (a), microbial biomass nitrogen (b), microbial biomass phosphorus (c), organic carbon (d), total nitrogen (e) and total phosphorus (f) in the soil under decaying logs in the decay classes (mean $\pm$ SD, $n = 5$). CK, control; DC1-DC5, decay classes I-V. Different letters indicate significant differences ($P < 0.05$) among the decay classes

Figure 2

Relative abundances (>1%) of fungi at the phylum (a) and genus (b) levels in the control (CK) and the decay classes (ranked by the sum of means). DC1-DC5, decay classes I-V. Data are the means of five samples for each group

Figure 3

The response of soil fungal community to decaying logs. Nonmetric multidimensional scaling (NMDS) analysis of the composition of soil fungal communities (a) based on Bray-Curtis distances. Heatmap of

soil fungal functional groups (b) from different decay classes of logs. CK, control; DC1-DC5, decay classes I-V

Figure 4

Fungal functional groups (guild) under different treatments (mean $\pm$ SD, n = 5). CK: blank control group. DC1-DC5: decay classes I-V. Different lowercase letters indicate significant differences (P < 0.05) among decay classes

Figure 5

Correlation heatmap of soil biochemical properties and the relative abundances of soil fungi at phylum (a) and genus (b) level. MBC: microbial biomass carbon, MBN: microbial biomass nitrogen, MBP: microbial biomass phosphorus, OC: organic carbon, TN: total nitrogen, TP: total phosphorus, WC: water content. * $P < 0.05$, ** $P < 0.01$

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